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NESTLING WEIGHT AND SURVIVAL IN INDIVIDUAL GREAT TITS (*PARUS MAJOR*)

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SUMMARY

(1) The aim of this paper is to estimate the shape of the curve relating first year survival to nestling weight in individual great tits (*Parus major*) and to study the causality of this relationship.

(2) Data were collected in a mainland and an island population. Nestlings were weighed and sexed in the nest when 2 weeks old. A recapture programme provided data for recapture-rate estimates in the winter. Local survival until next breeding season was estimated by capturing the breeding population. Brood-size manipulation experiments were performed in the mainland population in order to manipulate nestling weights.

(3) The relation between local recapture rate and nestling weight was described using logistic regression techniques. The descriptive model included positive weight and negative squared weight regression coefficients, if controlled for year, sex and date. Recapture rate approached zero at weights of *c.* 70% of the adult body weight. The curves for both populations showed an approximately linear part over a rather long range of weights. At high weights, the curve levelled off in the mainland population and curved down in the island population.

(4) Survival from weighing till fledging and recapture rate from fledging till winter were related to nestling weight, but recapture rate from winter till breeding was not.

(5) The effect of brood-size manipulation on nestling weight and subsequent recapture rate suggests causality of the recapture rate–nestling weight curve. Additional information from a comparison of the association between recapture rate and nestling weight within and between broods leads to the conclusion that weight does play a causal role in this relationship. Recapture rate–nestling weight curves can thus be estimated from non-experimental data.

INTRODUCTION

In order to evaluate optimization theories on reproduction, empirical studies should assess costs and benefits in terms of the ‘reproductive value’ (Fisher 1930) as a function of reproductive decisions (Daan *et al.* 1989). Such functions can only be measured in the field, where pressures of natural selection operate. Once they are known it is possible to predict how an individual should behave in order to maximize its reproductive value.

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The relationship between nestling weight and subsequent nestling survival is of particular interest. If it is causal, weight differences between nestlings can be taken as fitness differences, an essential step to relate parental investment to fitness (Nur 1984b, 1987; Tinbergen *et al.* 1987).

In the great tit (*Parus major* L.), birds of low weight as nestlings had low recapture rates (Perrins 1965; Dhondt 1971; Garnett 1981) and a lower chance of acquiring a territory (Drent 1983). Low nestling weights indicate slow growth due to malnutrition, and may be correlated with a number of fledgling traits. Heritability estimates of nestling weights are low (van Noordwijk, van Balen & Scharloo 1988). Nestling weight therefore can best be regarded as an estimator of a complex of traits affected by malnutrition.

The classic study by Perrins (1965) was one of the first examples showing nestling survival as a function of nestling weight. Perrins suggested that this function is convex in some years and concave in others. Such variations will affect the selection pressures on clutch size, and are therefore of great importance. However, it is doubtful whether nestling weight is the causal factor, as Perrins found both a seasonal change in nestling weights and a strong relationship between hatching date and recapture rate. In years when nestling weights at first increased and later decreased during the season there was a concave relationship, whereas in the years of continuous decrease of nestling weights there was a convex relationship, implying an effect of hatching date on the shape of the curve. Thus, there remains an alternative explanation: hatching date affects both nestling weight and local survival rate independently, whereas nestling recapture rate is independent of nestling weight.

This complication may be overcome by conducting field experiments that manipulate the reproductive decision studied for individual birds. Brood size manipulation experiments have frequently been carried out to assess effects of the intensity (brood size) of current reproduction on components of parental fitness (see Lessells 1986 and Dijkstra *et al.* 1990 for reviews). Experiments manipulating brood size in tits have shown that increased brood sizes cause low nestling weights as well as low recapture rates (Nur 1984a; Tinbergen 1987; Smith, Källander & Nilsson 1987; Lindén 1988). However, the fact that nestlings in enlarged broods were both lighter, and survived less well does not necessarily mean that the experimental weight decrease causes the decrease in survival. Using the survival–nestling weight curve to estimate survival may lead to the wrong conclusions.

In this paper we therefore evaluate the evidence for causality of the relationship between recapture rate and nestling weight in data obtained in a mainland population and an island population of great tits.

Two hypotheses about the causality of the recapture rate–nestling weight relationship can be formulated. The first and most simple one is that the weight of the nestling directly causes the relationship with recapture rate (weight hypothesis, Fig. 1a). Under this hypothesis, effects of parental quality or environmental factors cause lowered nestling weight which, in turn, cause lowered survival of the nestlings. The other hypothesis is that parental quality, brood size and/or environmental factors (henceforth called ‘brood traits’) have simultaneous but independent effects on nestling weight and on differential mortality (trait hypothesis, Fig. 1b). In other words, the young of broods in, for example, poor environments may be fed to low weights. The survival rate of these young may be less because survival after fledging is affected by the poor environment, and not because they have low body weights.

There are two approaches to distinguish between these hypotheses, one experimental and the other descriptive.

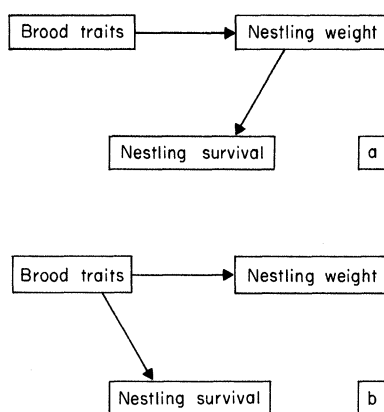


FIG. 1. Possible causal pathways in the determination of survival under (a) the weight hypothesis, and (b) the trait hypothesis.

Firstly, the experimental approach. When we manipulate brood size, both recapture rate and nestling weight are affected strongly, as has been shown by many authors (for references see above). As broods have been chosen at random we expect no differences in initial brood traits between the experimental groups. If recapture rate is only causally related to nestling weight (weight hypothesis) we expect the within-manipulation effects of nestling weight on recapture rate to be indistinguishable from the between-manipulation effects of nestling weight. If nestling recapture rate is only causally related to brood traits (trait hypothesis) we expect the within-manipulation group trends to be predictable by weight (as these may reflect brood traits) but the between-manipulation recapture rates should not differ. If both causal pathways are involved, we expect the within-manipulation group effect of nestling weight on recapture rate to be stronger than the between-manipulation group effect. A similar analysis in Nur (1984a) suggests that the weight hypothesis holds for blue tits (*Parus caeruleus* L.).

However, there is the possibility that brood size manipulations affect parental and/or environmental quality (food depletion), that in turn affect survival independently of nestling weight. To investigate this we compared intra- with interbrood variation. As brood traits would affect all nestlings within a brood equally, the association between recapture rate and weight within broods must be independent of brood traits, whereas the between-brood variation might be dependent on brood traits. Under the weight hypothesis we would, for the linear part of the curve, expect the derivative of the recapture rate–weight curve for a mean brood weight to be identical to the derivative of the within-brood recapture rate–weight curve when the mean brood weight was the same. Under the trait hypothesis we would expect the between-brood derivative to be different from the within-brood derivative, whereas the second one is expected to be zero.

In this paper, we first describe the relationship between recapture rate and nestling weight, then analyse when the weight-dependent mortality occurs, and thereafter discuss data relevant to the causality of this relationship. Finally, the general shape of the weight–survival relationship and its consequences are discussed.

METHODS

Data were collected from two ringed populations of great tits (*Parus major*), one in the Hoge Veluwe, situated on the mainland, and one on the island of Vlieland. The latter population is relatively isolated, and immigration rates there are much lower than on the mainland (Tinbergen, van Balen & van Eck 1985; van Balen, van Noordwijk & Visser 1987). Data are available from the years 1975–79 and 1983–86 for the Hoge Veluwe, and 1979–86 excluding 1984 (no young weighed) for Vlieland. Data analysis was restricted to first broods only. For details of the study areas see van Balen (1980) and Kluyver (1971).

In the Hoge Veluwe, all nestlings were ringed at about 7 days old and weighed on days 13, 14, 15 or 16 of their life between 11.00 h and 17.00 h. In 1975–79, nestlings were sexed on the day of weighing on the basis of the colour of their greater wing coverts and general colouring (Drent 1984). Sexing great tits in the nest is not absolutely reliable: in the Hoge Veluwe 89% of the recaptured males ($n=456$) and 78% of the recaptured females ($n=354$) had been sexed correctly as nestlings. On Vlieland these figures were 85% for both sexes ($n=421$ females and 426 males). The accuracy in sexing computed in this way was not weight-dependent.

Brood size manipulations were undertaken in the Hoge Veluwe in the years 1983–86. The manipulations were performed on the second day of nestling life. Three nests with approximately the same clutch size and hatching date were selected and half of the young from one nest were transferred to a second nest; a third nest was kept as a control. Nests with low hatching success were not included. For further details see Tinbergen (1987).

Winter recapture rate was established using different methods: monthly night checks of nest-boxes for sleeping birds, mist netting and reading colour rings of birds foraging on beech mast or at an artificial feeder. The birds were attracted to the mist nets using feeding tables baited with sunflower seeds in the years 1975–79; water and decoys were used in the years 1983–86. In addition, in both periods two mist-netting sites with feeding tables adjacent to the study area were used. Weather permitting, 2 days each week were spent netting birds. Recaptures were thus roughly confined to the study area and should be regarded as estimates of local survival.

All birds recaptured or seen in November and December are taken as winter recaptures. Recapture as a breeding bird was based on catches of breeders in the study area in the following year.

On Vlieland all nestlings were ringed, sexed and weighed around day 15 of nestling life. Here, only survival till breeding was assessed. In both study areas almost all breeding birds were identified each breeding season.

The data were organized in groups characterized by nestling weight (groups of 1 g), date, sex and year. Logistic regression using the GLIM statistical package (Numerical Algorithms Group 1987) was used to estimate probabilities of local recapture as a function of nestling weight. The logistic regression is designed to describe proportions as a function of one or more independent variables. The regression gives a maximum likelihood estimate of the exponent a in the function $e^a/(1+e^a)$. Variables, if not significant, were dropped subsequently from a model including all variables to be tested. Tests of significance were performed on the difference in deviance (a measure of residual variation) between a model with and without the variable or factor included. This difference in deviance (delta deviance) is χ^2 distributed with the difference in degrees of freedom between the models as its degrees of freedom (MacCullagh & Nelder 1984).

TABLE 1. Logistic regression for Vlieland and the Hoge Veluwe relating breeding recapture probability to nestling weight (g), squared nestling weight (g^2), sex (two levels, female = 1, male = 2), year (7 and 5 levels), date (early = 1, average = 2, late = 3) and the interactions of year and sex with weight. The scale deviance for the null model represents the variation if no independent variables are included in the model. Estimates for the derivatives and the constant term are computed in a model including all significant factors and given for an average year. For further explanation see text

Variable	Vlieland			Hoge Veluwe		
	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient
Null model	422.22	350		290.66	257	
Constant			-26.72			-23.77
Weight	28.38***	1	2.963	17.90***	1	2.279
Weight ²	22.32***	1	-0.0872	6.16**	1	-0.060
Sex	7.34**	1	-3.550	N.S.		—
Sex \times weight	6.44**	1	0.1948	N.S.		—
Year	43.62***	6		70.78***	4	
Year \times weight	N.S.			N.S.		
Date	N.S.			N.S.		

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

RESULTS

Relationship between recapture rate and nestling weight

Logistic regressions for breeding recapture rate on nestling weight were computed for nestlings from first broods in the years without manipulations. Breeding recapture rate (S_{nb} , survival from nest to breeding) was defined as the probability that an individual nestling was recaptured as a breeding bird.

Nestling weight, squared nestling weight and hatching date were taken as independent variables. Hatching date was included by dividing nestlings for each year into three equally sized groups according to their hatching date (early = 1, average = 2 and late = 3). Year was included as a factor (un-ordered group), with 5 (Hoge Veluwe) or 7 (Vlieland) levels.

Nestling male great tits are on average c. 1 g heavier at 14 days than females (Dhondt 1971; Drent 1984) and tend to have higher recapture rates. This may be due to the higher dispersal rate of females (Greenwood, Harvey & Perrins 1979). We made no correction for wrong sex determinations and included sex at weighing as a factor with two levels in the analysis. For Vlieland, 3675 young were included in the analysis; for the Hoge Veluwe, 3575.

In both study areas there was a significant association of recapture rate with weight, weight² and year (Table 1). This means that, if corrected for annual differences in level of recapture rate, a quadratic logistic regression fitted the data better than a linear one. In the Hoge Veluwe, sex and date did not add significantly to the fit, nor did the interactions with weight. In Vlieland, both sex and the interaction between sex and weight were significant, implying sex differences in the shape of the curve. No association with date or an interaction between year and weight existed in the Vlieland population.

Estimates of the regression coefficients were computed in a model including the significant variables. To give one model for an average situation a correction for the

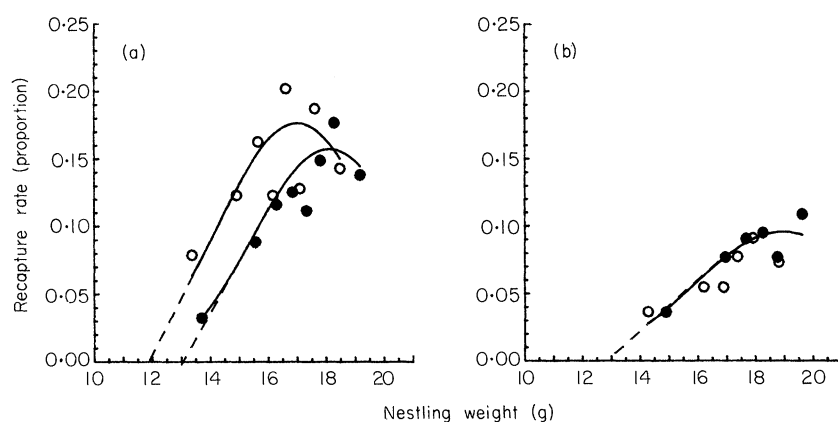


FIG. 2. Relationship between breeding recapture rate (S_{nb}) and first brood nestling weight in (a) Vlieland (1979–86) and (b) the Hoge Veluwe (1975–79). Curves represent the logistic fit as given in Table 1, broken lines give the extrapolation from the linear part of the curve towards recapture rate = 0. Data points are given for females (○) and males (●) separately. Vlieland: $n = 215$ (males), 203 (females); Hoge Veluwe: $n = 221$ (males), $n = 220$ (females) per data point. The recapture rates are plotted against the average weight of the nestlings.

average year was included in the estimate of the coefficient. The resulting curves are shown for both areas in Fig. 2.

The difference in level of the recapture rates between the two areas is probably related to differences in dispersal rate between the island and the mainland population. Sex differences are found in Vlieland but not in the Hoge Veluwe, possibly also caused by differences in dispersal between the sexes.

All curves steadily increase with nestling weight, flatten off and even tend to curve downwards at high nestling weights. As the significance of the quadratic weight term in the regression may be based on the lower rather than the higher weights, we checked whether the curve really has a negative slope for high nestling weights. Linear logistic regression was performed of recapture rate on nestling weight for the higher nestling weights, controlled for sex and year. In the Hoge Veluwe the slope for nestling weights over 18 g did not deviate significantly from zero. On Vlieland, this relationship in nestlings of over 17.5 g had a negative slope ($b = -0.359$, delta deviance = 5.627, d.f. = 1, $P < 0.025$). Heavy nestlings on Vlieland were thus less likely than those of average weight to breed in the area the next year.

For the same reason we checked whether the Hoge Veluwe curve really flattens off. We performed two regressions for breeding recapture on nestling weight controlled for year and sex, one for the nestlings weighing ≥ 17.5 g and the other for those weighing < 17.5 g. Weight, year and sex were included as independent factors. The derivatives for weight were significantly different (difference between derivatives = 0.3565, 95% confidence interval of the difference = 0.0331), proving that the curve does flatten off.

When does weight-dependent mortality occur?

In order to analyse when the weight-dependent mortality occurs, we analysed local survival rates over three shorter intervals: from weighing to fledging (S_{nf} = survival probability from weighing in the nest to fledging), from fledging until November and

TABLE 2. Logistic regressions for the Hoge Veluwe relating fledging rate (S_{nf}), winter recapture probability from birds fledged (S_{fw}) and breeding recapture probability from birds captured in November and December (S_{wb}) to nestling weight (g), squared nestling weight (g^2), sex (two levels, female = 1, male = 2), year (7 and 5 levels), date (early = 1, average = 2, late = 3) and the interactions of year and sex with weight. For further explanation see Table 1 and text

Variable	S_{nf}			S_{fw}			S_{wb}		
	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient
Null model	407.3	257		339.34	244		182.45	128	
Constant			-18.68			20.55			-0.491
Weight	161.5***	1	2.384	30.09***	1	2.327	N.S.		—
Weight ²	10.0**	1	-0.0532	9.72**	1	-0.0618	N.S.		—
Sex	6.3*	1	-0.5008	13.47***	1	0.4372	N.S.		—
Sex \times weight	N.S.		—	N.S.		—	N.S.		—
Year	14.7***	4		61.47***	4		36.4***	4	
Year \times weight	15.3**	4		18.71**	1		N.S.		
Date	N.S.		—	4.58*	1	-0.1476	N.S.		—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

December (S_{fw} = survival probability from fledging till winter) and from the winter period until breeding (S_{wb} = survival probability from winter till breeding). The first of these measures is a true estimate of survival, because no dispersal occurs during this period. The other two estimates combine dispersal away from the study area with mortality. The analysis was performed on the Hoge Veluwe data for the years 1975–79. For S_{nf} , 3575 young were included in the analysis, for S_{fw} , 3467, and for S_{wb} 402.

Survival from weighing till fledging (S_{nf}) was significantly related to nestling weight, nestling weight², sex and year (Table 2). In this case, there was also a significant year–weight interaction. This means that the curves relating S_{nf} to nestling weight differed in level with sex (female above male) and in shape with year. Estimates of the regression coefficients given in Table 2 are corrected for the average year effect. The logistic fit of this curve is shown for both sexes in Fig. 3.

Recapture rate from fledging till winter (S_{fw}) is significantly related to nestling weight, nestling weight², sex, year and has a year–weight interaction. In contrast to S_{nf} curves, males have higher S_{fw} curves than females. The fit is shown in Fig. 3 for the sexes separately and for average year values.

To check whether the slope of the S_{fw} curve flattens off at high nestling weights more than would be expected from a linear logistic curve, we performed two regressions for S_{fw} on nestling weight controlled for year (included in the analysis): one for the nestlings weighing ≥ 17.5 g and the other for those weighing < 17.5 controlled for year and sex. The derivatives for weight were significantly different (difference between derivatives = 0.2971, 95% confidence interval of the difference = 0.0267).

The recapture rate for the period from winter until breeding (S_{wb}) is not related to nestling weight. Only annual differences can be shown in the logistic regression (Table 2). The mean annual level of survival is plotted in Fig. 3.

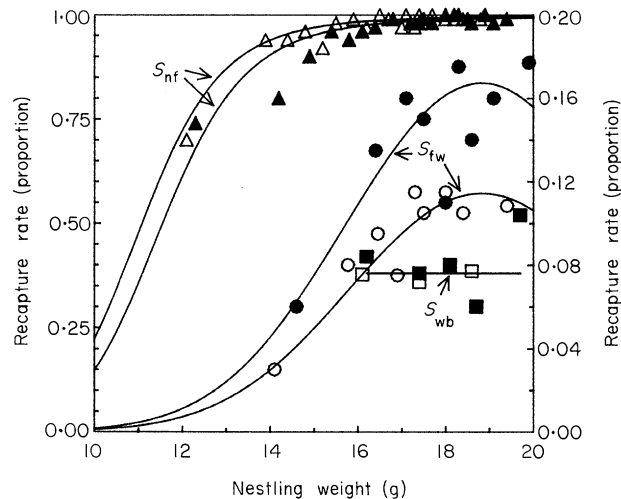


FIG. 3. Recapture rate for first brood nestlings of the Hoge Veluwe as a function of nestling weight for different periods of the year: triangles = survival in the nest from weighing until fledging (S_{nf}); circles = recapture rate in November and December of fledged nestlings (S_{fw}); squares = breeding recapture rate of those birds that had been caught in the previous November and December (S_{wb}). Open points represent nestlings sexed as females, closed points nestlings sexed as males. Numbers of observations per point: S_{nf} = 45 for the three lowest weights per sex and 90 for the higher weight categories; S_{fw} = 193, S_{wb} = 50. Lines are logistic fits, as given in Table 2. Note that S_{nf} and S_{wb} are given on the left and S_{fw} on the right y-axis.

The weight-dependent selection thus occurred in the nest (S_{nf}) for the very low nestling weights, and between fledging and winter (S_{fw}) over a large range of nestling weights. After mid-winter (S_{wb}) there was no longer a weight-dependent selection. This conclusion was also drawn by Perrins (1963) for the Wytham great tits, but without controlling for sex and date.

The value of S_{nb} predicted from the product of the separate S_{nf} , S_{fw} and S_{wb} and for the sexes separately, is considerably lower than that measured directly. This is because some birds, particularly females, survived locally to breeding but were not recaptured in winter. As females are lighter than males, the shape of the recapture rate–nestling weight curve for the combined sexes is expected to be biased towards the male shape if deduced from winter estimates.

To check this, we analysed in more detail the nestling weights of the birds recaptured as a breeding bird. These birds were categorized according to (i) sex and (ii) whether or not they had been caught in November or December. Nestling weights of these groups were significantly different, but this weight difference could be explained by sex alone. Inclusion of the recapture history did not reduce the deviance of the model. Thus, if allowance is made for sex, estimates of the shape of the recapture rate–weight curves from different periods of recapture were consistent.

Causality of the weight-dependent recapture rate

Experimental approach

To test whether nestling weight explains recapture rate independently of manipulation category (see Introduction), we analysed recapture rates from weighing until November and December (S_{nw}) in 4 years of experimental data from the Hoge Veluwe (1983–86). We

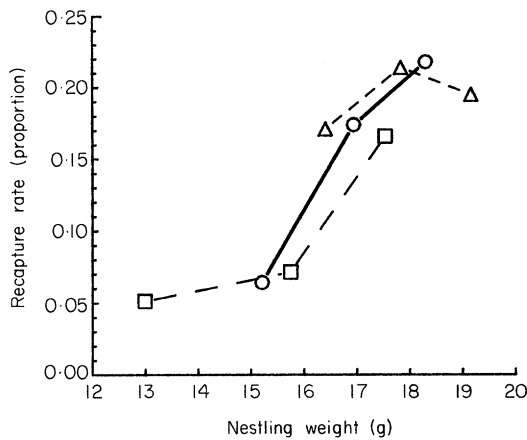


FIG. 4. Local recapture rate as a function of nestling weight in broods with manipulated size (Hoge Veluwe 1983–86). Symbols correspond to manipulation categories (squares = enlarged broods, circles = control broods, triangles = reduced broods). For further explanation see text.

determined whether manipulation explained additional variance, when year, nestling weight and nestling weight² were included as variables explaining recapture rate. This was not the case (Δ deviance = 2.40, d.f. = 1, N.S.). The same result was obtained for the breeding recapture rate (S_{nb} , Δ deviance = 0.05, d.f. = 1, N.S.), independent of whether or not the number of young fledged was included in the analysis. This means that the weight trend in the recapture rate did not differ for the different experimental groups. To show this graphically, each experimental group of young (enlarged, reduced, and control broods) was divided into three roughly equally sized groups on the basis of their weight. Recapture rates for these subgroups are plotted in Fig. 4.

The trait hypothesis would not predict this result, unless it could be argued that manipulation affected brood traits as parental condition or food availability, although no effects of brood-size manipulation on parental weight (Tinbergen 1987) and survival were found.

Descriptive approach

To eliminate this possibility we compared within-brood and between-brood effects of nestling weight on recapture rate (see Introduction). We analysed the recapture rates of breeding birds for Vlieland (1979–86, excluding 1984) and both the recapture rates for winter and breeding (1975–79) for the Hoge Veluwe. Each young was characterized by the year it was born, its sex in the nest, the mean weight of the brood it came from, and the difference between its weight and the mean weight of the brood. Logistic regressions were computed for these characters (Table 3). Because of the complexity of the shape of the weight–recovery rate relationship, the analysis was done for restricted parts of the curve. For the Vlieland data, the analysis was restricted to the nestlings from broods with a mean weight below 17 g. Estimated derivatives for between- and within-brood association of recapture rate with nestling weight are very close and statistically not different (S.E. 0.050 and 0.061, respectively). The data are shown in Fig. 5. For the winter recapture data for the Hoge Veluwe (restricted to mean brood weight < 18 g), the conclusion is the same (S.E. = 0.090 and 0.090 for between- and within-broods, respectively). Moreover, for the

TABLE 3. The comparison of within-nest weight effects with between-nest weight effects on recapture probability. Comparisons are given for Vlieland (S_{nb}) and for the Hoge Veluwe (S_{nw} , S_{nb}). Logistic regressions were computed for the different recapture probabilities including as independent factors: mean brood weight (= mean weight, g), the difference between the nestling weight and its mean brood weight (g), sex (two levels, female = 1, male = 2) and year (resp. 7, 5 and 5 levels). For further explanation see table 1 and text

Variable	Vlieland (S_{nb})			Hoge Veluwe (S_{nw})			Hoge Veluwe (S_{nb})		
	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient	(Delta) deviance	(Delta) d.f.	Estimate of the coefficient
Null model	434.29	380		216.81	257		316.98	336	
Constant			-4.859			-7.741			-7.126
Mean weight	16.72***	1	0.2439	13.50***	1	0.3201	22.09***	1	0.2597
Delta weight	16.93***	1	0.2126	13.88***	1	0.3254	3.93*	1	0.1396
Sex	7.13**	1	-0.4102	14.27***	1	0.4937	N.S.		
Year	49.97***	6		26.13***	4		71.71***	4	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

higher mean brood weights both estimates decrease strongly and do not significantly differ from zero. For the breeding recovery in the Hoge Veluwe area we had to include the group with a mean brood weight of 19 g in order to find significant trends. In this case the two did not differ significantly (S.E. between-broods 0.058, within-broods 0.071).

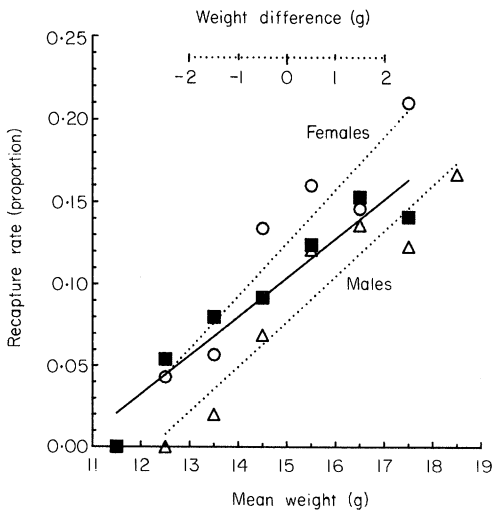


FIG. 5. Nestling weight as a causal factor in the determination of recapture rate on Vlieland. Closed squares give between-brood comparison: local recapture rate of nestlings is plotted against the mean nestling weight of their brood (x-axis, bottom). Open symbols give the within nest comparison: local recapture rate of nestlings is plotted against the difference between their weight and the average weight of their brood (x-axis, top). Circles = females, triangles = males. For further explanation see text.

TABLE 4. A comparison of fitness curves for nestling weight from the literature. GT=great tit, BT=blue tit, HV=Hoge Veluwe. Recapture methods: a=mist-netting, b=evening checks of nest-boxes in winter, c=recaptures as a breeding bird. The column 'controlled for' indicates whether the following variables were included in the analysis: y=year effects, d=date effects, s=sex effects

Species	Area	Years	Sex	Min weight	Flattens off?	Curves down?	Survival till	Catching method	Source	Controlled for
GT	HV	5	Male	13	Yes	No	Nov, Dec	a,b,c	This study	y,d,s
GT	HV	5	Female	13	Yes	No	Nov, Dec	a,b,c	This study	y,d,s
GT	HV	5	Male	13	Yes	No	Breeding	c	This study	y,d,s
GT	HV	5	Female	13	Yes	No	Breeding	c	This study	y,d,s
GT	Vlieland	7	Male	13	Yes	Yes	Breeding	c	This study	y,d,s
GT	Vlieland	7	Female	11.5	Yes	Yes	Breeding	c	This study	y,d,s
GT	Ghent	3	Male	13	No	No	3 months onw.	a,b,c	Dhondt 1971	s
GT	Ghent	3	Female	12.5	Yes	No	3 months onw.	a,b,c	Dhondt 1971	s
GT	Wytham	2	Mixed	16	No	No	3 months onw.	a,b,c	Garnett 1981	—
GT	Wytham	6	Mixed	13	?	No	3 months onw.	a,b,c	Perrins 1965	—
BT	Wytham	2	Mixed	?	Yes	No	3 months onw.	a,b,c	Nur 1984a, b	—

Within-brood derivatives were thus indistinguishable from between-brood derivatives of recapture rate on weight, indicating that weight indeed plays a causal role in determining recapture rate. Thus, the weight hypothesis fits the data best.

This is an important conclusion as it implies that, in natural broods, we may use nestling weight as an estimator for recapture rate, independently of brood traits such as parental quality or environment. It does not mean that brood traits have no effect on survival at all, but that they act via nestling weight.

DISCUSSION

Causality

We conclude that nestling weight is causally related to subsequent recapture rate of the nestlings. This is important as it allows us to use the relationship to estimate fitness of nestlings. Nestling weight can thus serve as an easy-to-measure step in the estimation of the fitness of a brood, as previously done by Nur (1984b, 1987) and Tinbergen *et al.* (1987). Moreover, we can estimate the survival nestling weight curve using data from unmanipulated broods, increasing the body of available data considerably, and enabling us to study the effects of external factors on the curve. The shape of the curve indicates selection pressure on nestling weight, and differences in the curve between populations or species may suggest reasons for differences in clutch size or nestling weight between areas.

Potential biases for shape

Few curves relating recapture rate to nestling weight have been published, and all have been based on tits (Table 4 and Fig. 6). The studies all found a positive association between recapture rate and nestling weight. However, when discussing the shape of curve found in the different studies we have to recognize that estimates of survival after fledging combine mortality with dispersal away from the study area. This leads to the following potential biases.

(a) Date-dependent local recapture rate. In some areas local recapture rate strongly declines with hatching date. The evidence suggests that late-hatched young are more

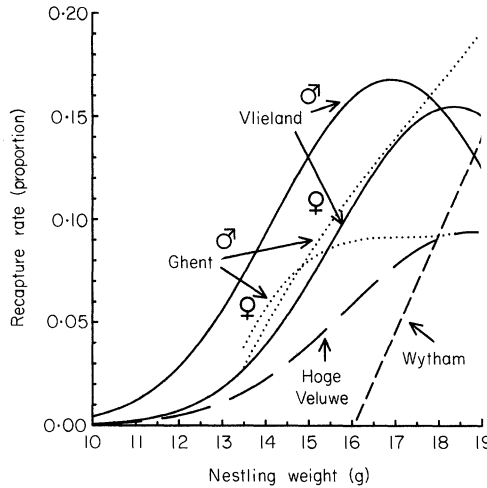


FIG. 6. Fits of the curves relating recapture rate to nestling weight for different populations: Vlieland (—); Hoge Veluwe (—); Ghent (·····) (Dhondt 1971); Wytham (---) (Garnett 1981). For Vlieland and Hoge Veluwe a logistic fit is given (Table 1), for Ghent a third-order polynome through the average data, and for Wytham a straight line. For more details see Table 4.

likely to disperse (Kluyver 1971; Dhondt 1971). If, in addition, nestling weight depends on date, the resulting shape of the nestling weight–recovery curve may be strongly affected. This may be the case in the Wytham data. In the data discussed in this paper we did not find date effects, partly due to the fact that we concentrated on first brood nestlings, and also because we work in woods with relatively low tit density.

(b) Sex-dependent recapture rate. Fewer females are recaptured than males, especially in winter (Dhondt 1971; this paper), and the weight of female nestlings is lower than that of males. If sex is not controlled for, the slope of the recapture rate–weight curves may be overestimated.

(c) Year-dependent recapture rate. If nestling weights as well as recapture rates vary between years in association with each other (cf. Drent 1984), the shape of the resulting curve will be affected when years are combined. If this positive association is not caused by nestling weight itself, a bias is introduced. One should therefore control for year.

(d) Weight-dependent dispersal. If dispersal is weight-dependent, the shape of the estimated curve will be affected. There is evidence both for (Drent 1984) and against (Kluyver 1971; Dhondt 1971) weight-dependent dispersal. None of the studies have taken this into account.

(e) Weight-dependent recapture. If recapture probability of live great tits is associated with their nestling weight, the estimated curve would also be affected. Heavier nestlings might, for instance, become relatively heavy birds and be more likely to be caught at feeders where fighting for food occurs. Therefore, we compared the shapes of the curves based on recaptures in winter (nightly nest-box checks and mist-netting at feeders) and during the breeding season. No differences were found, suggesting that this is not a serious problem.

None of the studies reviewed above (Table 4, Fig. 6) excluded all of the sources of bias, and the lack of control for some of these biases, notably in the data for Wytham and Ghent, makes comparisons of the studies difficult.

The data set from Garnett (1981) differs from the others in that minimum weight for survival is higher (16 g), which may not be representative for all years, e.g. Perrins (1965) found lower minimum weights. The general shape of the recapture rate–nestling weight curve is described best by a minimum weight for survival (*c.* 70% of adult body weight), a linear increase and, in most cases, flattening off at higher weights. The Vlieland data set is probably the least biased of all because dispersal on this island is low, as judged by the high breeding recapture rate of locally born young and the low immigration rate. Differences in shape of the recapture rate–nestling weight curves between the sexes are likely to be general.

Furthermore, the level, as well as the shape, of the curves is dependent on the dispersal rate. This is a general problem in the estimation of the fitness of a brood. In future we should use recovery data from the national ringing scheme, or work in very large study plots to tackle this problem.

The shape of fitness curves used in optimal allocation models (Kacelnik 1989) and in dynamic programming (Mangle & Clark 1988) relating a state variable to fitness resembles the shape of the empirical curves described here. In detail, the shape differs in that recapture rates of nestlings tend to be almost linearly related to weight and then have a short trajectory of weights where the survival rate curve flattens off, or even curves down.

Mechanisms

There are several possible mechanisms underlying the shape of the survival–nestling weight curves. Perrins (1965) suggested that nestling weight is correlated to energy reserves, and Garnett (1981) showed that heavy great tits did have relatively more fat and protein, and calculated that these reserves would last starved birds about a day. It is not known whether this is important to the newly fledged great tit.

Alternatively, nestling weight may affect dominance status. Drent (1983) showed that there is a relationship between male nestling weight and the probability of acquiring a territory. Heavier males tend to become dominant in the juvenile group competing for territories. Similarly, there is a relationship between body size (tarsus) and the proportion of interactions won (Garnett 1981). The reduced survival probabilities of the heavier nestlings on Vlieland implies stabilizing selection for weight, even when there are no parental costs. Price & Grant (1984) found evidence for selection favouring small body size in *Geospiza fortis* between 2 and 10 months old. They suggest that large juveniles may have a metabolic disadvantage. In great tits, one possible mechanism is that dispersal is positively related to weight. However, the effect does not occur in the mainland population, making dispersal a less likely explanation. Being heavy may have other disadvantages, particularly in situations where being dominant does not increase access to food. Heavy birds might be excluded from some foraging microhabitats, have higher metabolic requirements or may be more vulnerable to attack by predators.

Consequences for optimal clutch size

Optimal clutch size or optimal parental investment can be predicted if both the fitness of the clutch and that of the parents is known in relation to clutch size. The maximal fitness is at the size of the clutch where the derivatives of both curves are equal but opposite in sign (Charnov & Krebs 1974). Changes in the shape of the recapture rate–nestling weight curve affect the shape of the fitness curve on clutch size and in turn affect

optimal clutch size, optimal fledging weights and optimal parental investment. Consequently, one would expect that clutch size should depend on the sex of the nestlings, as female curves are steeper than male curves.

Measuring both the clutch and parental fitness curves empirically as a function of the ecological context will be an important task for the coming years. Advancement along these lines will depend on the estimate of global as opposed to local survival in order to account for observed variations in breeding ecology.

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